

# A NEW MITRATE FROM THE LOWER ORDOVICIAN OF SOUTHERN FRANCE

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**ABSTRACT.** The mitrocystitid mitrate *Vizcainocarpus dentiger* gen. et sp. nov. originates from the Lower Arenig of the Montagne Noire, France. Its distinctive features are two dorsal areas of polyplated integument, thorn-like projections on the postero-ventral head plates and a leftward-opening mouth. A preliminary cladistic analysis shows that *V. dentiger* is more derived than *Chinianocarpus thorali* and is the most primitive mitrocystitid with a differentiated centro-dorsal plate D12 and with the upper lip plate rigidly incorporated in the skeleton.

THE aims of this paper are to reconstruct and describe a new genus and species of mitrocystitid mitrate from the south of France, and to determine its systematic position. The new form belongs to the diversified fauna of 'stylophoran carpoids' from the Lower Arenig of the Montagne Noire (Thoral 1935; Ubaghs 1961, 1969, 1983, 1991, 1994; Smith 1988; Cripps 1989b; Daley 1992). Five or six other lower Ordovician mitrates are known from this region: *Peltocystis cornuta*, *Chinianocarpus thorali*, *Lagynocystis* cf. *pyramidalis*, *Ovocarpus moncereti*, *O.?* *circularis* and an undescribed peltocystidan mentioned by Ubaghs (1991, p. 157).

Jefferies' calcichordate theory is followed herein. According to this theory, mitrates are primitive members of the three chordate subphyla Acraniata, Tunicata and Craniata. The mitrate described in this paper is a mitrocystitid (*sensu* Caster 1952). The Mitrocystitida are paraphyletic (Jefferies 1986; Beisswenger 1994) and regarded by Jefferies as stem-group craniates. The reasons for this are explained thoroughly elsewhere (Jefferies 1967, 1968, 1986; Jefferies and Lewis 1978; Cripps 1990; Beisswenger 1994).

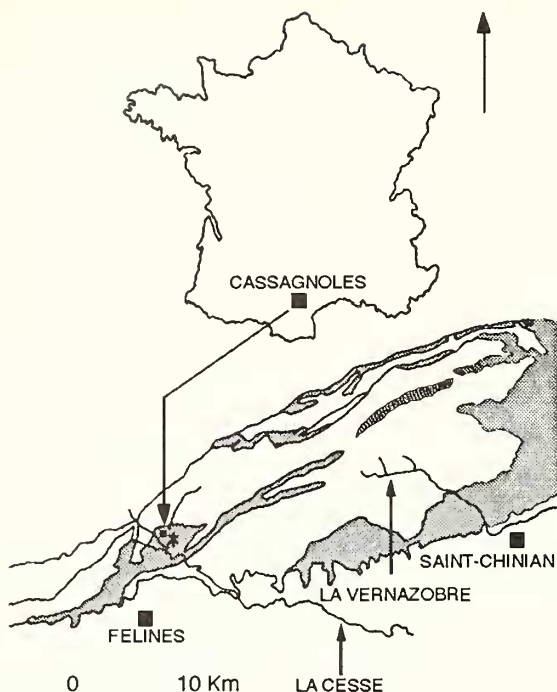
Mitrates are covered with calcitic plates of echinoderm type and consist of an anterior, massive head, and a posterior, articulated tail. The internal anatomy of the head can be compared, in Jefferies' view, with that of such primitive living chordates as amphioxus and the tunicates. In particular, the mitrocystitid mitrates would share with modern craniates a lateral line system and dorsal, touch-sensory branches of the trigeminal nerves.

## MATERIALS AND METHODS

*Material, horizon and locality.* A broken siliceous nodule showing the external aspect of the dorsal and ventral head skeleton, and part of the tail of a single individual, here designated as the holotype (specimens IPM-B 49101a and IPM-B 49101b; Institut de Paléontologie, Museum National d'Histoire Naturelle, Paris). The internal anatomy is unknown.

The approximate position of the collecting site locality is shown in Text-figure 1 (reference map for France: IGN, 1:25000; Labastide-Rouayroux 2444-Ouest; co-ordinates: x = 623, 370, y = 3120, 150). The fossils come from the stratigraphical level known as 'faunizone f' (Montagne Noire, France). This level consists of dark, micaceous, sandy or silty shales covered with a rusty crust and containing black siliceous nodules of different shapes and sizes (Courtesole *et al.* 1982, 1985). The 'faunizone f' occupies most of the formation known as Schistes de Saint-Chinian and is of early Arenig age (Capéra *et al.* 1978).

Although a correlation with other localities yielding Arenig sequences is difficult, the trilobite and graptolite associations of 'faunizone f' may indicate an earlier age than that of the earliest

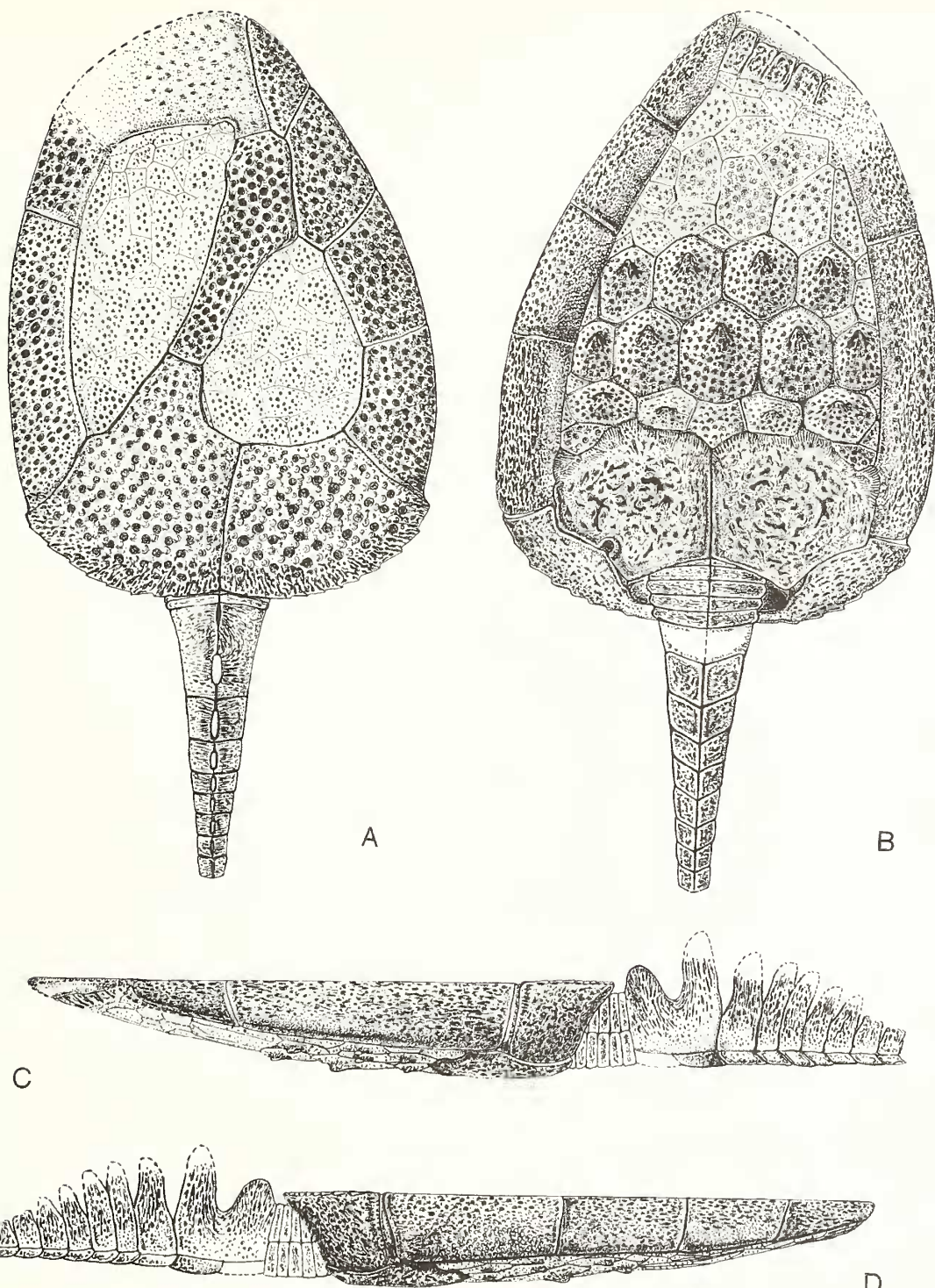


TEXT-FIG. 1. Map of the southern side of the Montagne Noire. Stippled areas to the north of Saint-Chinian, Félènes and the River Cesse mark the extent of lower Ordovician rocks. The approximate position of the locality where the fossils were collected is indicated by an asterisk. Reference map for France: IGN, 1:25000; Labastide-Rouayroux 2444-Ouest; coordinates:  $x = 623,370$ ,  $y = 3120,150$  (redrawn and simplified after Ubaghs 1969).

recognizable Arenig beds in Wales. Fortey and Owens (1987) pointed out that a continuous Tremadoc/Arenig sequence in the British Isles is lacking. The lowermost beds of the incomplete Moridunian Stage in Wales incorporate the *Merlinia selwynii* Biozone. In the Montagne Noire, the level *f* includes, among the other taxa, the trilobites *Asaphelina barroisi*, *Euloma filacovi*, *Megistaspis filacovi* and *Symphysurus angustatus*, the graptolites *Clonograptus* cf. *persistens*, *Dictyonema* cf. *murrayi* and *Tetragraptus amii*, the articulate brachiopods *Orthambonites roquebrunensis* and *Pleurorthis fascis* and the inarticulate brachiopods *Spondyglossella spondylifera* and *Conotreta turricula* (Courtessole *et al.* 1982).

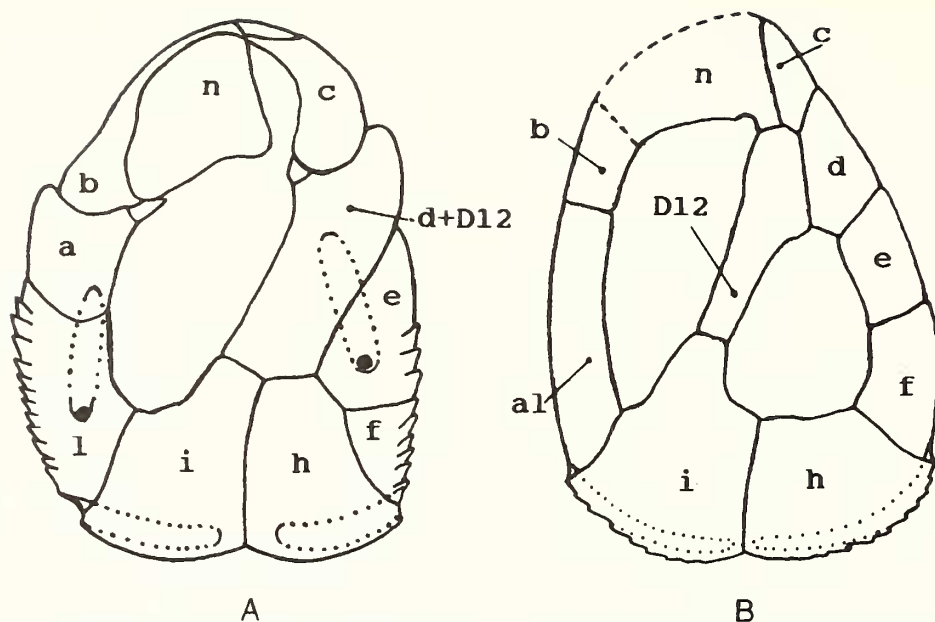
The Schistes de Saint-Chinian have yielded well-preserved and articulated skeletons (mainly of echinoderms), regardless of the size and texture of the skeletal elements. This suggests relatively rapid burial of the organisms and limited post-mortem transport. The cornute and mitrate fauna from the Montagne Noire includes, to date, 22 species and represents, together with the radiate echinoderms, '... un des ensembles fauniques les plus diversifiés que l'on connaisse' (Ubaghs 1994, p. 108; see also Smith 1988). However, individual specimens are very rare. According to Ubaghs (1969), this rarity is presumably due to preservational bias and to the fact that only isolated nodules have been collected regularly over the past decades, whereas an accurate study of the nodule-bearing sediments has long been neglected.

*Methods.* The specimens were cleaned in ethanalamine thioglycollate. IPM-B 49101b was partly dissected to expose the partial external mould of the tail. The reconstruction of *Vizcainocarpus dentiger* (Text-fig. 2) is based on *camera lucida* drawings of latex casts coated with ammonium chloride.



TEXT-FIG. 2. Reconstruction of *Vizcainocarpus dentiger* gen. et sp. nov. in A, dorsal, B, ventral, C, left lateral, and D, right lateral views.





TEXT-FIG. 3. Plate nomenclature in *Chinianocarpus thoralis* and *Vizcainocarpus dentiger*. A, reconstruction of the head of *C. thoralis* in dorsal aspect (redrawn after Jefferies 1986). B, reconstruction of the head of *V. dentiger* in dorsal aspect. Drawings not to scale.

#### SYSTEMATIC PALAEOLOGY

Superphylum DEUTEROSTOMIA Grobбен, 1908

(Stem group of the Craniata?)

Family *Incertae sedis*

Genus *VIZCAINOCARPUS* gen. nov.

*Derivation of name.* After M. Daniel Vicaïno of Carcassonne, France, who discovered the fossil described herein, for his outstanding contributions to the palaeontology of the Montagne Noire. The suffix *-carpus* means a fruit (Greek, *karpōs*).

*Type species.* *Vizcainocarpus dentiger* sp. nov., the only species known.

*Diagnosis.* Two dorsal areas of polyplated integument; centro-dorsal plate D12 in contact posteriorly with a process projecting from plate i and anteriorly with plates c, d and n; mouth opening leftward and limited ventrally by oral platelets of different shapes and sizes; anterior half of ventral head skeleton with irregular plates; posterior half consisting of hexagonal plates with a conical process bending forward; stereom texture of the marginal, dorsal and ventral integument plates highly porous; peripheral external surface of plates e and f, external surface of plate n and of the oral platelets with coarse texture; ridges of fibrillar stereom visible along the dorsal margins of the styloid blades and the hind-tail ossicles; lateral line opening surrounded by a semicircular thickening and close to the posterior margin of plate e.



*Vizcainocarpus dentiger* sp. nov.

Plates 1–2; Text-figures 2–8

*Derivation of name.* The specific name alludes to the tooth-like processes on the postero-ventral head plates (Latin, *dentiger* = tooth-bearer).

*Diagnosis.* As for the genus, by monotypy.

## ANATOMICAL DESCRIPTION

*Head*

The plate nomenclature implies homology with like-named plates in cornutes such as *Reticulocarpus hamusi* and *Prokopicystis mergli*, and in mitrates such as *Barrandeocarpus norvegicus* and *Mitrocystella incipiens* (Jefferies and Prokop 1972; Craske and Jefferies 1989; Cripps 1989a, 1991; Cripps and Daley 1994). The head is about 6 mm long and 4 mm across at its widest point. *V. dentiger* is, therefore, significantly smaller than most other known mitrates, its size being comparable to that of such 'dwarf' cornutes as *Beryllia miranda*, *Domfrontia pissotensis*, *Nanocarpus dolambii* and *Prokopicystis mergli* (Ubaghs 1991; Cripps and Daley 1994). It is not known whether the small size of *V. dentiger* is related to its ontogenetic age or is a specific feature of this mitrate.

The head is roughly pyriform in outline. Its left side is less convex externally than its right side. The dorsal surface is flat, whereas the ventral surface is gently convex. The height of the head is greatest near the tail junction and decreases uniformly towards the mouth opening. The most anterior part of the dorsal skeleton and the left anterior angle of the head are poorly preserved. Four marginal plates on the right and two marginal plates on the left are visible. A large, asymmetrical plate n lies anterior to the left integument area. Plates h and i are the largest dorsal plates, whereas  $\epsilon$  and  $\theta$  are the largest ventral plates.

*Dorsal skeleton.* The dorsal skeleton consists of nine marginal plates, a centro-dorsal plate D12 and two areas of polyplated integument, one on the left and one on the right of D12 (Text-figs 2A, 3B; Pl. 1, fig. 1; Pl. 2, figs 1–2). The posterior and lateral marginal plates show a flat dorsal and a curved ventro-lateral part.

Plates h and i build the posterior third of the dorsal skeleton. They differ in shape and size, and are wider posteriorly than anteriorly. The suture between them bends gently rightward. The postero-dorsal margin of both plates is convex rearward and bears seven or eight shallow 'teeth'. Each tooth has a longer, gently sloping median side and a shorter, steep lateral side (Text-fig. 2A; Pl. 1, fig. 1; Pl. 2, fig. 2). Plates h and i are in contact with the rearmost lateral marginal plates of the right and left side, respectively, along two antero-laterally concave sutures (Text-fig. 2C–D; Pl. 1, fig. 1).

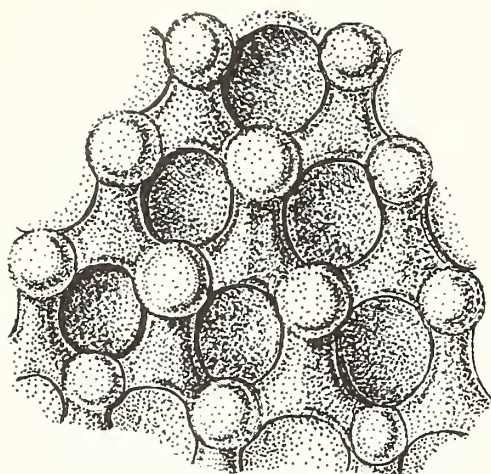
The anterior margin of h is slightly concave forward. The anterior margin of i carries a stout process directed anteriorly and rightward. The left margin of this process is almost straight, whereas its right margin is concave. The process is sutured with the posterior margin of D12 (Pl. 1, fig. 1; Pl. 2, fig. 2).

Two shallow, peripheral grooves run along the posterior margins of h and i without changing their width and almost reach the dorsal mid-line (Text-figs 2A, 3B). Their position and extent are marked by an abrupt change in the histology of the calcitic skeleton near the posterior margin of the head (Pl. 1, fig. 1; Pl. 2, fig. 2). The peripheral grooves straddle the sutures formed by h and i with the rearmost right (f) and left (al) marginal plates, respectively. Here, they turn downward and continue as vertical, shallow depressions along the lateral head walls just behind the vertical projections of the i/al and h/f sutures (Text-fig. 2C–D).

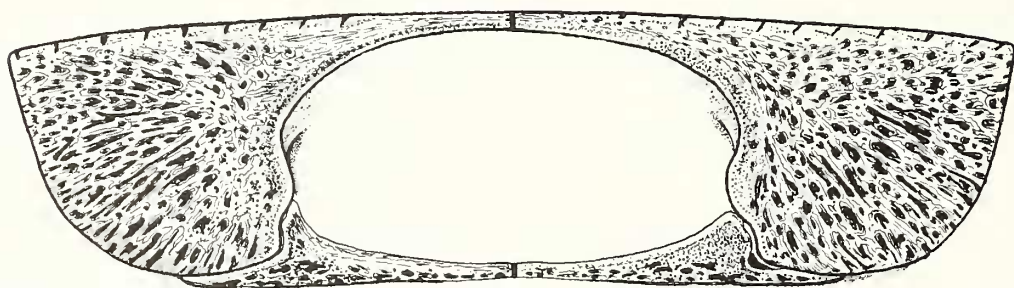
Most of the dorsal external surface of h and i shows regularly spaced, sub-circular, stereom pores delimited by thick trabeculae (Text-fig. 4; Pl. 2, fig. 2). Near the anterior, lateral and median margins of h and i and on the anterior process of i the pores are slightly smaller. At the level of the peripheral grooves they become slit-like and irregular in outline and the trabeculae which delimit them are twisted. Near the median end of each peripheral groove, the pores and trabeculae run obliquely rearward and laterally. Near the lateral ends of both grooves, most trabeculae and pores form a right angle with the main body axis (Pl. 2, fig. 2).

The downward projections of h and i form most of the posterior head surface (Text-fig. 5; Pl. 1, fig. 2) and slope slightly forward and downward. Their external surface shows a compact stereom. Sinuous ridges and irregular striations are also visible along their dorsal margins.

Four marginal plates frame the right side of the head (Text-figs 2A, 3B; Pl. 1, fig. 1) and are identified as f, e, d, and c on the basis of a comparison with *Chinianocarpus thoralis* (Text-fig. 3A; see also Cripps 1990). Plate f has a convex lateral margin and is slightly wider posteriorly than anteriorly. Its postero-lateral angle bears



TEXT-FIG. 4. *Vizcainocarpus dentiger* gen. et sp. nov. Reconstruction of the stereom texture of the marginal plates (based mainly on plate i).



TEXT-FIG. 5. *Vizcainocarpus dentiger* gen. et sp. nov. Reconstruction of the posterior aspect of the head.

a notch corresponding to the point where the most anterior part of the right peripheral groove straddles the posterior end of the h/f suture and bends downward (Pl. 1, fig. 1).

Plate e is sub-trapezoidal and occupies the central part of the right margin of the head (Pl. 1, fig. 1).

Plate d is pentagonal and is in contact with e posteriorly, c anteriorly and the most anterior part of D12 medially (Pl. 1, fig. 1; Pl. 2, fig. 1). The suture between D12 and d runs almost parallel to the main body axis.

Plate c, the smallest dorsal marginal element, lies just right of the dorsal mid-line. Its posterior third is inserted between D12 and d. Its anterior third lies right of plate n (Pl. 1, fig. 1; Pl. 2, figs 1, 5).

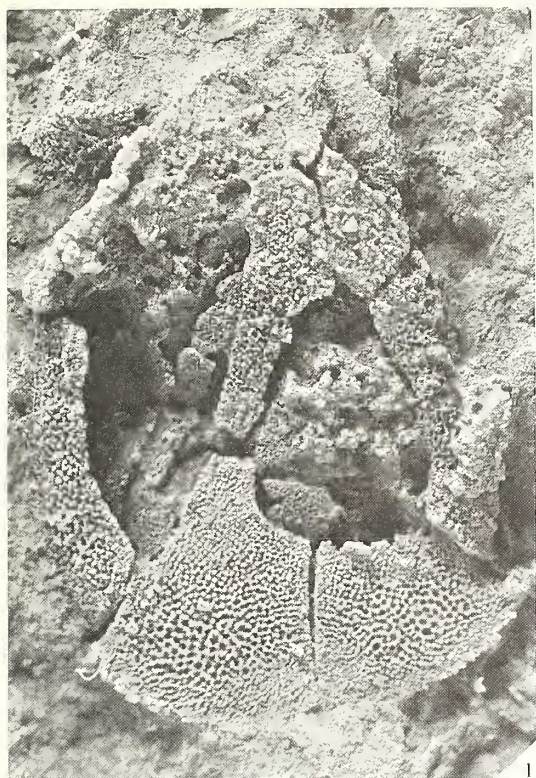
On the left side of the head two marginal plates are visible (Text-figs 2A, 3B; Pl. 1, fig. 1). The anterior plate, poorly preserved and best observed in ventral view (Pl. 1, fig. 2), occupies the left anterior angle of the head and perhaps corresponds to plate b in *C. thorali* (Text-fig. 3A).

A single, elongate plate frames most of the left side of the head posterior to b. This plate, labelled as al, is gently convex externally. Like f, al shows in dorsal view a notch near its postero-lateral angle, marking the position of the most anterior part of the left peripheral groove (Text-figs 2A, 3B; Pl. 1, fig. 1). Plate al corresponds in position to a and l in *C. thorali*, but it is difficult to say whether it is homologous with one or the other of these elements or whether it results from their fusion.

#### EXPLANATION OF PLATE I

Figs 1–4. *Vizcainocarpus dentiger* gen. et sp. nov.; Level f, Schistes de Saint-Chinian (Lower Arenig); Cassagnoles, Montagne Noire, France; latex casts. 1, IPM-B 49101a; dorsal head skeleton;  $\times 14$ . 2–4, IPM-B 49101b. 2, ventral head skeleton;  $\times 14$ . 3, fore-tail rings and styloid blades in left lateral view;  $\times 40$ . 4, hind tail in left lateral view;  $\times 40$ .









TEXT-FIG. 6. *Vizcainocarpus dentiger* gen. et sp. nov. Camera lucida drawing of the most anterior part of the ventral head skeleton showing the lower lip plates arranged along a slanting line;  $\times 20$ .

An isolated skeletal fragment is visible both dorsally and ventrally in front of the left anterior angle of the head (Pl. 1, figs 1–2). The fragment consists of two sloping surfaces. The highly porous stereom texture of one of these surfaces is very similar to that of the dorsal surface of h and i. The fragment is perhaps part of a posterior marginal element of a different individual, but its identification is uncertain.

The stereom texture of all marginal plates except n consists of larger pores in a central position, and smaller pores towards their median dorsal margins and near the sutures with adjacent plates.

The upper lip plate n is asymmetrical in outline and comparable in relative size, shape and position to its namesake in *C. thoralii* (Text-fig. 3; Pl. 1, fig. 1). Although the preservation is poor, its posterior margin is partly visible in front of the left dorsal integument area. Its anterior margin runs from left of c to right of b and is anteriorly convex. The n/c suture is represented by a faint sinuous line (Pl. 1, fig. 1; Pl. 2, fig. 1). In *C. thoralii*, a short, narrow area of integument is present between n and c (Text-fig. 3A). This area consists of two or three small plates and projects anteriorly from the integument comprised between the left marginal plates and the anterior half of the oblique ridge complex (Jefferies and Prokop 1972, pl. 7, fig. a; Jefferies 1986, p. 291; Cripps 1990, p. 37). In *V. dentiger*, n is in contact with D12 along the most anterior part of the latter (Pl. 1, fig. 1; Pl. 2, fig. 1).

D12 in *V. dentiger* can be readily homologized with its namesake in other mitrocystitid mitrates on the basis of its position. This plate runs obliquely from anterior right to posterior left, dividing the dorsal skeleton into two subequal fields. D12 is comparatively narrower in *V. dentiger* than in all the other mitrates in which this element is differentiated as a separate plate, and consists of two parts. The anterior part is rectangular in outline and is in contact with c, d and n. The posterior part is narrow and elongate and is in contact with the anterior process of i along a short suture. Although D12 and i appear as separate elements (Pl. 1, fig. 1; Pl. 2, fig. 2), this is probably the result of mechanical displacement and not of breakage, as the posterior end of D12 and the anterior end of the process of i show articulation facets along which these plates were originally in contact. In *C. thoralii*, D12 is not a separate plate and d sends out a median flange corresponding to the anterior half of the oblique ridge complex. This flange is sutured with an extension of plate i directed anteriorly and rightward (Text-fig. 3A).

The stereom texture of D12 in *V. dentiger* is similar to that of the marginal elements. Most of the centro-dorsal surface of this plate bears widely spaced pores. Along its margins the stereom texture is slightly coarser, in that the pores are similar and more irregular.

The two areas of polyplated integument separated by D12 differ in size and shape (Pl. 1, fig. 1). The left area is better preserved, as a small number of plates have maintained their original position. The integument plates are thin and very irregular in shape, although in some cases this may be the result of breakage, and their stereom texture is retiform. Some of the plates in contact with the left margin of D12 are elongate. The left integument area is delimited on the left by the median margins of a1 and b, posteriorly by the left margin of the process of i, on the right by the left margin of D12 and anteriorly by the posterior margin of n. The right integument area is delimited on the left by the right margin of D12 and by the right margin of the process of i, posteriorly by the anterior margin of h, on the right by the median margins of c and f, and anteriorly by the postero-median margins of d.

The dorsal skeleton does not show other openings.

*Ventral skeleton.* The ventral skeleton includes the oral platelets, the plates of the head floor, and the postero-ventral plates  $\epsilon$  and  $\theta$ . The downward bending portions of the dorsal marginal elements are also visible ventrally (Text-figs 2B, 6–8; Pl. 1, fig. 2; Pl. 2, figs 3–5).

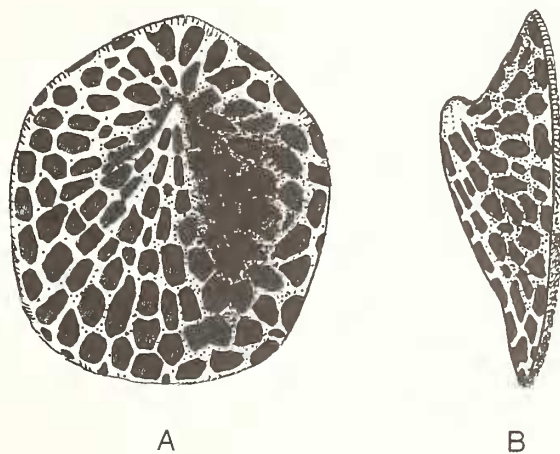
Five oral platelets arranged along a slanting line are visible. The right angle of the mouth opening is anterior to the left one (Text-fig. 6; Pl. 2, fig. 5). Perhaps one or two other platelets were present in life near the left angle of the mouth opening, but the preservation is too poor to allow the exact number of these elements to

be detected. The platelets are roughly equal in length, but differ in width. The two rightmost platelets are narrow, rectangular elements about half as wide as long. The third platelet is slightly wider, whereas the fourth and fifth platelet are about twice as wide as the first two and are sub-trapezoidal. The external surface of the platelets is rough in texture. The platelets are flexibly articulated with the most anterior head floor plates (Pl. 1, fig. 2; Pl. 2, figs 3, 5). The integument area lying just behind the lower lip probably corresponded to the buccal cavity in life.

The remaining ventral head plates can be divided into two groups: a smaller, anterior group of irregular elements and a larger, posterior group of polygonal plates. The plates of the anterior group do not seem to overlap each other nor do they overlap the more anterior, smaller elements framing the posterior margin of the oral platelets. The plates of the anterior group have irregular shape and arrangement. Those which are closer to the lateral margins of the head are slightly narrower than those which occupy a more median position (Pl. 1, fig. 2; Pl. 2, fig. 3).

The plates of the posterior group form three transverse rows (Pl. 1, fig. 2; Pl. 2, fig. 3). They are roughly hexagonal and possess a stout, conical process inclined forward (Text-fig. 7). The size of the processes is

TEXT-FIG. 7. *Vizcainocarpus dentiger* gen. et sp. nov. Reconstruction of a postero-ventral head plate in A, external and B, left lateral views.



apparently related to that of the plates bearing them. On the smaller, lateral plates of each of the three transverse rows the processes are knob-like and have an almost symmetrical outline in lateral view. The distal ends of these processes are formed by the fusion of a number of trabeculae.

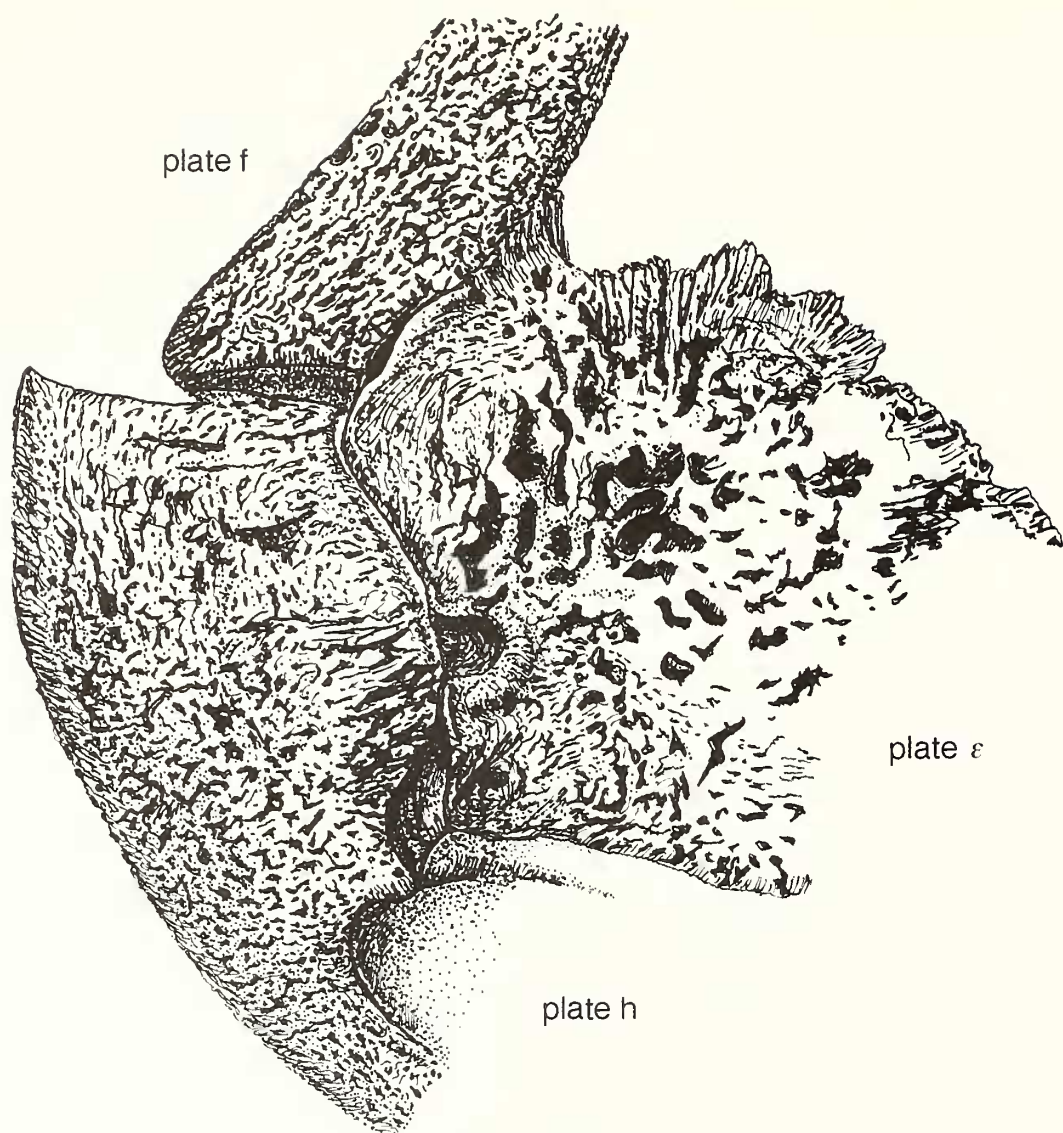
It is difficult to reconstruct the number of elements in each row, especially near the lateral margins of the head, where the plates are considerably displaced. In the first row, four hexagonal plates are visible. The two admedian plates are about twice as large as the lateral ones. The left lateral plate is poorly preserved and its process is not clearly visible.

The second row consists of five hexagonal plates, all of which carry a robust process. The two admedian plates are as large as the admedian plates of the anterior row. The lateral plates of the second row are smaller than the lateral plates of the first row. The mid-ventral plate is the largest polygonal element of the postero-ventral skeleton.

In the third row, the two admedian plates and the left lateral plate show a minute process. The right lateral plate is poorly preserved. The plates of the third row are not regular in outline and are less well preserved than those of the first two rows.

A small element lying in front of the  $\varepsilon/\theta$  suture, apparently without a process, is likely to correspond to plate p of other mitrocystitids (Pl. 1, fig. 2; Pl. 2, fig. 3). Other small, irregular plates are present between the lateral elements of the first and second, and of the second and third, transverse rows, both on the left and on the right side of the head. Their precise arrangement cannot be reconstructed as accurately as that of the process-bearing plates.

The ventral plates show a highly porous stereom texture. The pores are generally irregular in shape and of different sizes even on the same plate, and are delimited by laterally compressed trabeculae that are oriented randomly. The posterior ventral plates show one or two circlets of elongate pores on the external surface of the tooth-like processes.



TEXT-FIG. 8. *Vizcainocarpus dentiger* gen. et sp. nov. Camera lucida drawing of the right postero-lateral angle of the head, showing plates  $\epsilon$ , h and f. The lateral line opening is visible on plate  $\epsilon$ ;  $\times 40$ .

The two largest ventral plates,  $\epsilon$  and  $\theta$ , are roughly trapezoidal and do not show a regular pattern in the distribution of pores and trabeculae (Text-figs 2B, 8; Pl. 1, fig. 2; Pl. 2, fig. 4). Plates  $\epsilon$  and  $\theta$  contribute to the lower half of the posterior head excavation and meet along a straight mid-ventral suture. Plate  $\theta$  slightly overlaps  $\epsilon$  in IPM-B 49101b. This is almost certainly due to a post-mortem mechanical displacement of the two plates relative to each other, since  $\theta$  bears a flat articulation facet along its median margin and is separated from plate  $\alpha 1$  by a gap.

A small sub-circular pit, visible at the centre of the posterior margin of  $\epsilon$  (Text-fig. 8; Pl. 1, fig. 2; Pl. 2, fig. 4), represents the opening of the lateral line system, according to Jefferies (1986). The remarkable aspect of this



opening in *V. dentiger* is its marginal position to  $\varepsilon$ . In all other mitrocystitids, the opening is anterior to the posterior margin of  $\varepsilon$ .

The external surface of  $\varepsilon$  and  $\theta$  is coarsely granular (Text-fig. 8; Pl. 2, fig. 4). The central area of each of these plates is occupied by twisted trabeculae which delimit irregular hollows. Around this area the trabeculae have a more regular arrangement, and tend to radiate towards the lateral, median and anterior margins of both  $\varepsilon$  and  $\theta$ . The anterior margins of  $\varepsilon$  and  $\theta$  show an irregular fringe of fibrillar stereom, whereas their posterior and postero-median areas are compact.

The rounded postero-lateral edges of  $\varepsilon$  and  $\theta$  fit into shallow grooves running along the ventral margins of the downward projections of h and i, and form with them a rocking articulation. This presumably allowed  $\varepsilon$  and  $\theta$  to move relative to h and i, respectively, in life. A similar articulation between  $\varepsilon$  and h and between  $\theta$  and i in *Eumityrocystella savilli* was described by Beisswenger (1994, p. 450) as a mechanism to 'allow the atrial openings to gape'. In *V. dentiger*, there are indications of the possible location of the left and right atrial openings where plates  $\varepsilon$ , h and f, and plates  $\theta$ , i and al, meet. The postero-lateral angles of the head were particularly flexible, as revealed by the morphology of the plate sutures (Text-fig. 8) in these regions.

Plates  $\varepsilon$  and  $\theta$  partly overlap the polygonal plates situated in front of them. They also overlap two small, intercalary plates at the postero-lateral angles of the ventral skeleton (Text-figs 2B, 8; Pl. 1, fig. 2). The anatomically left intercalary plate is inserted between  $\theta$  and al, whereas the right intercalary plate is inserted between  $\varepsilon$  and f.

## Tail

*Fore-tail.* The fore-tail skeleton (Text-fig. 2C–D; Pl. 1, figs 2–3) consists of five or six calcitic rings. Each ring is made of four plates. The dorsal plates seem to be flexibly articulated with the left ventral plates, but the nature of this articulation is difficult to reconstruct. No polyplated folds of integument between successive rings have been observed. The stereom of the rings consists of irregular striations oriented perpendicular to the longitudinal axis of the tail. Despite the poor preservation of the fore-tail, it is possible to observe that the rings are partly clenched ventrally without signs of breakage (Pl. 1, fig. 2).

*Mid-tail.* The styloid (Text-fig. 2C–D; Pl. 1, fig. 3) is a massive element. Its anterior blade has a semicircular outline. Its posterior blade is incomplete, but the preserved parts of its anterior and posterior margins are sharp. The stereom forms a series of fine striations along the dorsal margin of the anterior blade and on the preserved part of the posterior blade. The lateral styloid surfaces are slightly concave outward. Only one pair of plates has been found articulated with the styloid. These are rectangular elements with a coarse histology comparable to that of the hind-tail plates. The mid-tail plates are slightly larger than the hind-tail plates and, like these, they are obliquely oriented with respect to the longitudinal axis of the tail.

*Hind-tail.* Seven or eight articulated, partially preserved ossicles are visible (Text-fig. 2C–D; Pl. 1, fig. 4). The first ossicle is taller than and twice as large as the second and comparable in size to the posterior styloid blade. The ossicles are rectangular in lateral view and their posterior and ventral margins are sinuous. The ossicles decrease rapidly in height so that the preserved region of the hind-tail shows a vague morphological tripartition, although not so evident as in *Chinianocarpus thoralis*, *Peltocystis cornuta*, *Chauvelia discoidalis* or *Eumityrocystella savilli* (Jefferies 1986; Cripps 1990; Beisswenger 1994). Irregular striations are visible along the dorsalmost parts of the lateral ossicular surfaces. The styloid blades and the tail ossicles seem to have anterior and posterior cutting edges.

The ventral hind-tail plates are rectangular in outline and overlap each other antero-posteriorly. It is not possible to reconstruct the nature of the contact between ossicles and plates. The plates are obliquely oriented with respect to the longitudinal axis of the tail so that the two plates of each hind-tail segment would have formed a chevron in life with the apex pointing rearward, as in *Chauvelia discoidalis* (Cripps 1990).

## COMPARISONS

*V. dentiger* resembles *Chinianocarpus thoralis* in the outline of the head, in the shape, position and relative size of plate n, and in the presence of two shallow peripheral grooves running near the posterior margins of h and i. Like *C. thoralis*, *V. dentiger* has four right marginal plates, a process of plate i directed forward and rightward, and a sub-elliptical area of integument left of the oblique ridge complex.

*V. dentiger* differs from *C. thorali* in possessing a differentiated plate D12. The latter presumably derives from plate d, which in *C. thorali* sends out a projection directed leftward and rearward. This projection carries along its left margin the anterior half of the oblique ridge and contacts the anterior process of i. In *C. thorali*, this process is sutured with the left margin of h. In *V. dentiger*, D12 is completely separate from h and delimits in part the right dorsal integument. Unlike *C. thorali*, *V. dentiger* shows plate n locked rigidly to the head frame. The presence of a suture between n and b is only vaguely suggested in the available material of *V. dentiger*, but the n/c suture is clearly visible. Also, *V. dentiger* has a flexible lower lip, whereas the lower lip is rigid in *C. thorali*. Plate al in *V. dentiger* probably corresponds, at least topologically, to plates a and l of *C. thorali*. In the latter species, l is the longest of the three lateral marginal plates of the left side of the head. Plate al in *V. dentiger* frames most of the left margin of the head. It occupies the same position as a and l in *C. thorali*, and its median margin delimits the left side of the left integument area.

The presence of two dorsal areas of polyplated integument in *V. dentiger* is a character shared with *Aspidocarpus* and *Chauvelia*. In these forms, D12 contacts both the two most anterior marginals of the right side of the head and plate n (Ubaghs 1979; Cripps 1990). Like *Aspidocarpus* and *Chauvelia*, *V. dentiger* shows no signs of paripores. As in *Aspidocarpus*, *Chauvelia* and *Ovocarpus*, plates  $\varepsilon$  and  $\theta$  in *V. dentiger* overlap small, scale-like elements lying just median to the rearmost lateral marginals.

*V. dentiger* differs from *Aspidocarpus* and *Chauvelia* in that it has a smaller number of lateral marginal plates and a more asymmetrical head outline. Also, its mouth faces more distinctly leftward and its oral platelets lack an anterior process. As in most mitrocystitids, the downward projections of h and i in *V. dentiger* are visible ventrally. Plates  $\varepsilon$  and  $\theta$  in *V. dentiger* do not show postero-ventral transverse keels, whereas in *Ovocarpus*, *Chauvelia* and *Aspidocarpus*, these keels are evident and each of them delimits two areas of the external surface of  $\varepsilon$  and  $\theta$  with a different stereomic structure. Plates  $\varepsilon$  and  $\theta$  in *V. dentiger* contribute to a small portion of the posterior head surface, which is formed mainly by the downward projections of plates h and i. The suture between  $\varepsilon$  and  $\theta$  in *V. dentiger* is relatively long with respect to the size of these two plates. Among the mitrocystitids, this condition is found only in *Mitrocystella incipiens*. In all other mitrocystitids, the  $\varepsilon/\theta$  suture is relatively short, exceptionally so in *Aspidocarpus*, *Chauvelia* and *Eumitrocystella*.

*V. dentiger* resembles *Ovocarpus* in possessing a highly porous stereom on the dorsal side of the head. The stereom of the dorsal and ventral head plates of *Aspidocarpus* (Ubaghs 1979) and *Chauvelia* (Cripps 1990) has comparatively smaller pores. *V. dentiger* differs from *Aspidocarpus*, *Chauvelia* and *Ovocarpus* in that a porous stereom is also present on its marginal plates.

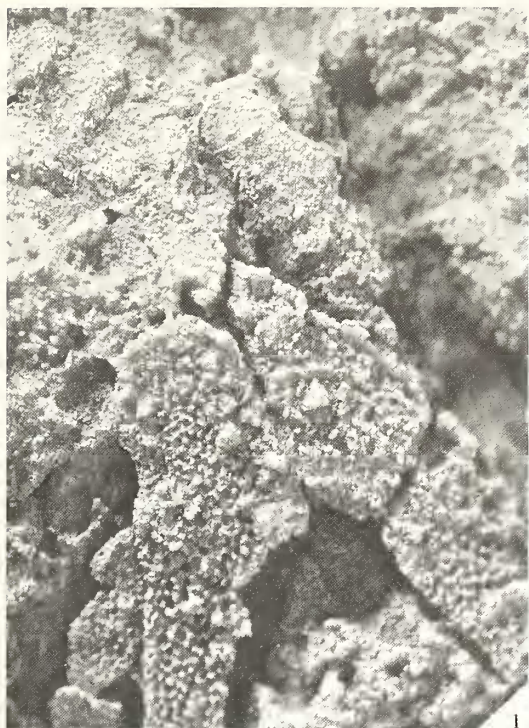
Cripps (1989a, 1989b) and Cripps and Daley (1994) proposed a progenetic mechanism to explain the small size and the contemporaneous presence of retiform stereom in such mitrate-like cornutes as *Beryllia miranda*, *Domfrontia pissotensis*, *Prokopocystis mergli* and *Reticulocarpus hanusi* (progenetic dwarfism). The relatively small size of such mitrates as *C. thorali* and *Peltocystis cornuta* is generally considered as an inheritance from their cornute ancestors, whereas the absence of retiform stereom is seen as a secondary loss in adult mitrates. Ontogenetic changes in the histology of the calcitic head plates have been observed in *Mitrocystites mitra*. Young individuals of this species show a typical retiform stereom (Jefferies 1968, pl. 8, fig. 5), sometimes partly replaced by a more compact stereom in the adults (Ubaghs 1967, fig. 328/7c).

The change in the stereom structure near the sutures of the marginal plates of *V. dentiger* is comparable to that observed in *Reticulocarpus hanusi* and *Prokopocystis mergli*. Jefferies and Prokop

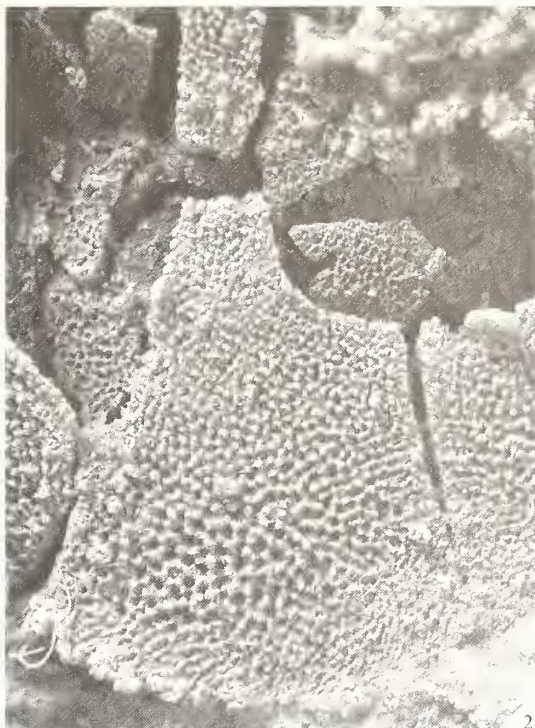
#### EXPLANATION OF PLATE 2

Figs 1–5. *Vizcainocarpus dentiger* gen. et sp. nov.; Level f, Schistes de Saint-Chinian (Lower Arenig); Cassagnoles, Montagne Noire, France; latex casts. 1–2, IPM-B 49101a;  $\times 26$ . 1, right antero-lateral region of dorsal head skeleton. 2, detailed aspect of plate i. 3–5, IPM-B 49101b;  $\times 20$ . 3, detailed aspect of ventral head skeleton. 4, postero-ventral aspect of head. 5, oral platelets.

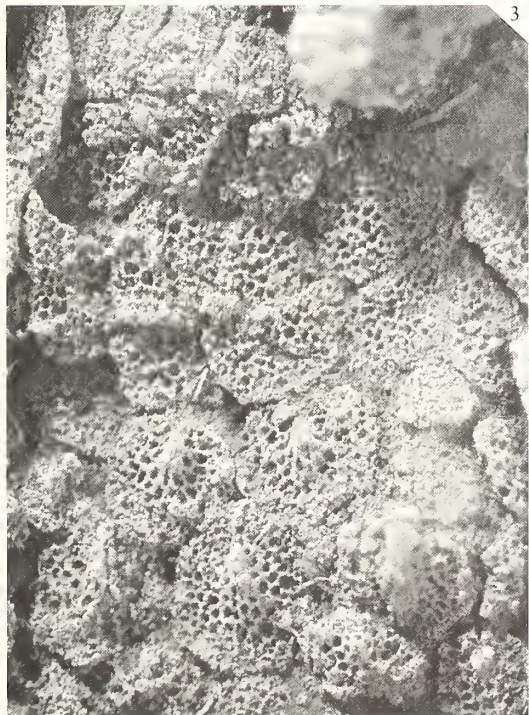




1



2



3



4



5



(1972, p. 80) interpreted the change in texture near the plate sutures of *Reticulocarpus hanusi* as a 'slowing-down of growth towards the end of life', and suggested (p. 72) that the preserved individuals of this cornute 'were not juvenile, but adult despite their small size'.

Small size and presence of retiform stereom on the integument plates also characterize the mitrate-like cornute *Nanocarpus dolanibii* (Ubaghs, 1991) and can perhaps be interpreted as a consequence of heterochronous evolution. Ubaghs (1994) reasoned that the presence of a wide-meshed stereom on the dorsal surface of the mitrate *Ovocarpus moncereti* is either a primitive or a neotenuous feature of this form.

On the basis of the available material of *V. dentiger*, it is difficult to say if this mitrate was characterized by dwarfism. Among mitrates, only *Ovocarpus? circularis* (Ubaghs, 1994) is comparable in size to *V. dentiger* and shows a similar retiform stereom.

### PHYLOGENETIC ANALYSIS

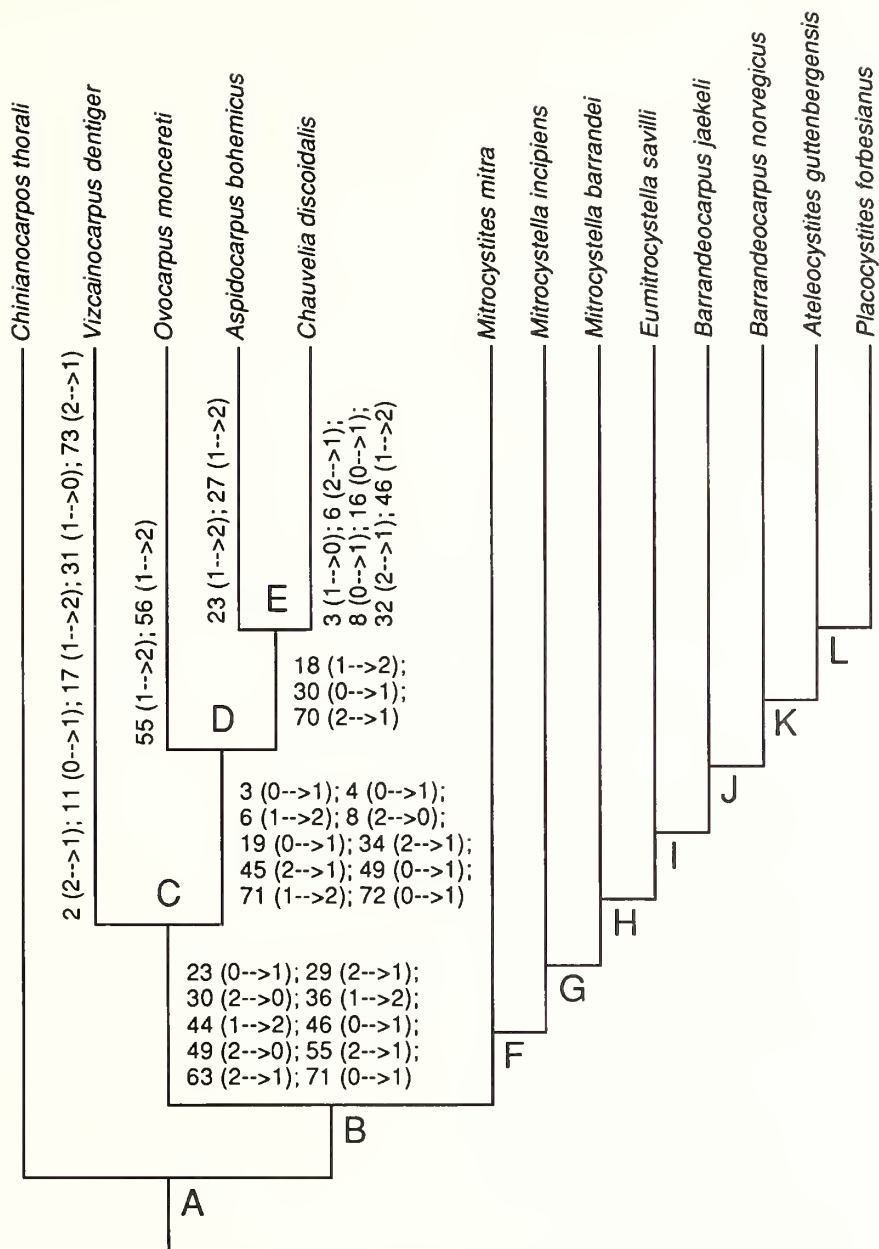
The character coding and most of the statistical aspects of the analysis (Text-fig. 9) will be thoroughly discussed elsewhere. In this section, I mainly focus on *V. dentiger*. Seventeen taxa and 76 characters were chosen (see Appendices 1 and 2). The taxa are: *Aspidocarpus bohemicus* (Ubaghs, 1979), *Ateleocystites guttenbergensis* (Kolata and Jollie, 1982), *Barrandeocarpus jaekeli* (Ubaghs, 1979), *B. novogicus* (Craske and Jefferies, 1989), *Chauvelia discoidalis* (Cripps, 1990), *Chinianocarpus thoralis* (Ubaghs, 1961), *Domfrontia pissotensis* (Cripps and Daley, 1994), *Emmitrocystella savilli* (Beisswenger, 1994), *Lagynocystis pyramidalis* (Jaekel, 1918), *Mitrocystella barrandei* (Jaekel, 1901), *M. incipiens* (Jaekel, 1901), *Mitrocystites mitra* (Barrande, 1887), *Ovocarpus moncereti* (Ubaghs, 1994), *Peltocystis cornua* (Thoral, 1935), *Placocystites forbesianus* (de Koninck, 1869), *Prokopicystis mergli* (Cripps, 1989a), *Vizcainocarpus dentiger* gen. et sp. nov.

The multistate coding in some taxa expresses uncertainty and is represented by states 1 or 2 in almost all cases, the only exception being character number 6 (0 or 2) in *Ovocarpus moncereti*. All characters were left unweighted and unordered. The cornutes *Domfrontia pissotensis* and *Prokopicystis mergli* and the mitrates *Lagynocystis pyramidalis* and *Peltocystis cornua* were used as outgroups to polarize the characters. The mitrates *Ateleocystites guttenbergensis* and *Placocystites forbesianus* were chosen as representatives of the anomalocystitids. The data were processed with PAUP 3.1.1 (Swofford 1993). The branch-and-bound search found one parsimonious tree (length = 195; CI = 0.687; RI = 0.777). The character-state optimization used was the accelerated transformation (ACCTRAN), which maximizes synapomorphies at each node and emphasizes reversals. The tree was rooted so as to make the outgroup paraphyletic with respect to the ingroup.

The position of *V. dentiger* (node C) is supported by ten state changes relative to characters nos 23 (0 → 1; CI = 1.000), 29 (2 → 1; CI = 1.000), 30 (2 → 0; CI = 0.667), 36 (1 → 2; CI = 1.000), 44 (1 → 2; CI = 0.500), 46 (0 → 1; CI = 1.000), 49 (2 → 0; CI = 0.667), 55 (2 → 1; CI = 0.400), 63 (2 → 1; CI = 1.000), 71 (0 → 1; CI = 1.000). *V. dentiger* shows a multistate coding for character numbers 28, 51, 58, 61 and 76, concerning the position of plate n with respect to the marginal plates, the nature of the contact between the dorsal and ventral fore-tail plates, and the morphology of the first hind-tail ossicle.

Some phylogenetic deductions from the cladogram are possible. The differentiation of D12 in *V. dentiger* led to the appearance of flexible integument areas over the left and the right pharynx. The widening of D12 reduced the relative extension of these areas (e.g. in *Aspidocarpus* and *Chauvelia*). Further reduction in the number of plates on both sides of D12 characterizes *Mitrocystites mitra*, in which the dorsal skeleton is completely rigid. In all other mitrocystitids and in the anomalocystitids D12 is expanded transversely and occupies most of the centro-dorsal skeleton.

The changes outlined above are perhaps linked with a number of modifications that occurred inside the mitrate head. These modifications would probably have mainly affected the pharynx. A particular feature of the mitrate head, the oblique groove, is important in this respect. According to Jefferies (1986), the oblique groove of mitrates separated the primary, left pharynx with the overlying left anterior coelom from the right anterior coelom. This groove runs obliquely across the



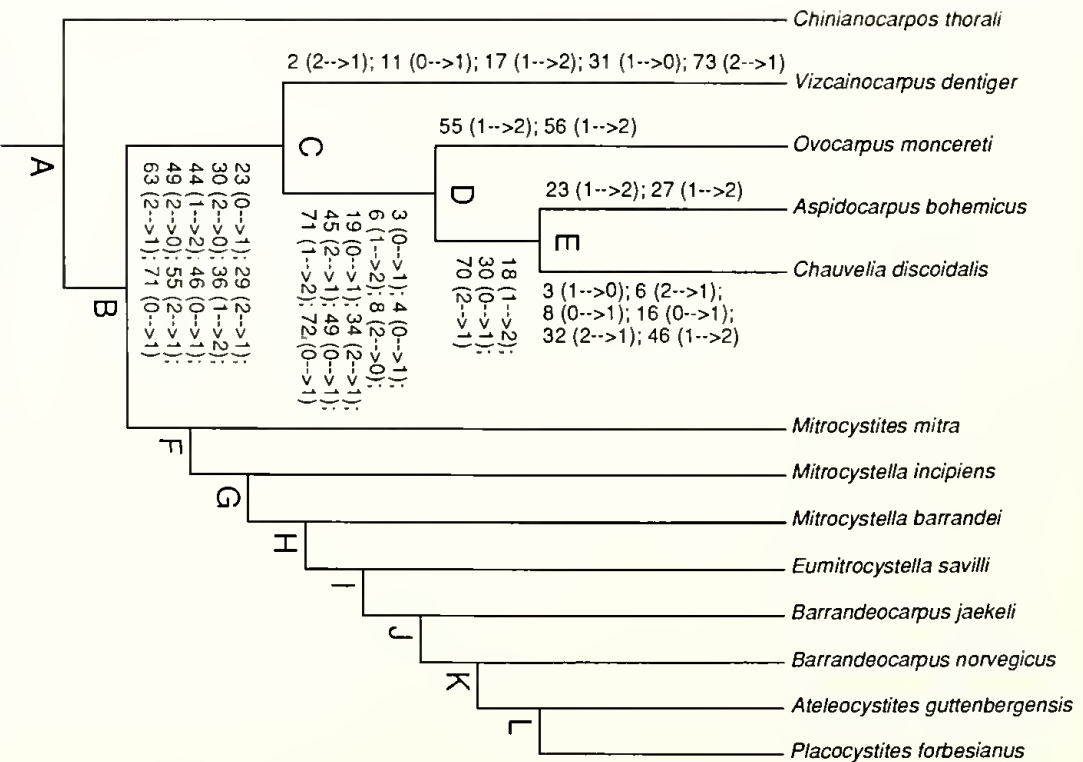
TEXT-FIG. 9. Interrelationships of the Mitrocystitidae. Numbers on the tree represent the synapomorphies supporting a particular node or the changes characterizing a particular branch. Only nodes C, D and E, which are relevant to the position of *Vizcainocarpus dentiger*, are described.

dorsal head steinkern and corresponds to an intercameral oblique ridge on the ventral surface of the dorsal skeleton.

In *Chinianocarpus thoralis*, the part of the dorsal head steinkern corresponding in position to the left pharynx is bigger than that corresponding to the anterior coelom plus the right pharynx. Also, the oblique ridge is straight and lies right of the patch of dorsal integument overlying the left







TEXT-FIG. 9. Interrelationships of the Mitrocystitidae. Numbers on the tree represent the synapomorphies supporting a particular node or the changes characterizing a particular branch. Only nodes C, D and E, which are relevant to the position of *Vizcainocarpus dentiger*, are described.

dorsal head sternum and corresponds to an intercameral oblique ridge on the ventral surface of the dorsal skeleton.

In *Clinimocarpus thorali*, the part of the dorsal head sternum corresponding in position to the left pharynx is bigger than that corresponding to the anterior coelom plus the right pharynx. Also, the oblique ridge is straight and lies right of the patch of dorsal integument overlying the left

pharynx (Jefferies and Prokop 1972, fig. 30, 3; pl. 14, fig. 1b). Although internal head anatomy is not known in *V. dentiger*, it is possible to deduce that the anterior half of the oblique ridge lay more to the left than in *C. thoralis*. The leftward displacement of the oblique ridge is more evident in *Aspidocarpus* and *Chauvelia*, which show a relatively wide, right dorsal flexible integument area. The position of the oblique ridge in these forms perhaps results from an enlargement of the second right pharynx, which, in turn, was accompanied by an increased pumping activity. In cladistically more derived mitrocystitids, it is possible to notice a general trend towards an increase in head size (e.g. *Mitrocystites mitra* and *Mitrocystella incipiens*). Perhaps as a consequence of the need for major stability during locomotion, the head roof became rigid. This rigidity was achieved through the widening of the dorsal head plates, which became less numerous. The latter process culminated with the presence of only two or three centro-dorsal plates in such forms as *Mitrocystella* spp., *Eumitrocystella savilli*, *Barrandeocarpus* spp. and the Anomalocystitida. A rigid ventral skeleton and a bilaterally symmetrical head (a condition exemplified by most Anomalocystitida) might also have been selected as a response to increased efficiency in locomotion.

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## APPENDIX 1

Description of the characters used in the phylogenetic analysis. For each character the different states are indicated by numbers in brackets. A discussion of the characters is given in the text.

1. Presence (1) or absence (0) of oral spines.
2. Postero-median extensions of peripheral grooves absent (0) or present and close to the postero-dorsal margins of the head (1) or not (2).
3. Antero-lateral extensions of peripheral grooves absent (0) or present and not extending (1) or extending (2) onto the second posterior marginal plate on both sides of the head.
4. Lateripores absent (0) or present and anterior to (1) or at the transverse level (2) of the postero-dorsal end of the h/i suture.
5. Presence (1) or absence (0) of paripores.
6. h/i suture straight and aligned with the tail axis (0) or bending rightward (1) or straight but not aligned with the tail axis (2).
7. Posterior margin of both h and i convex posteriorly (0) or with median excavation which occupies less than half (1) or more than half (2) of the maximum width of both h and i or straight (3).
8. Anterior margin of i not lying (0) or lying anterior to anterior margin of h and semicircular in outline (1) or not (2).
9. Projections of h and i visible in ventral view (1) or not (0).
10. h and i not in contact (0) or in contact with the most posterior lateral marginals (1) and with the postero-lateral ends of the sutures thus formed lying anterior (1) or posterior (2) to the postero-dorsal end of the h/i suture.
11. Presence (1) or absence (0) of serrations along the posterior margin of both h and i.
12. Presence (1) or absence (0) of serrations along the external margin of the rearmost right marginal plate.
13. Presence (1) or absence (0) of serrations along the external margin of the rearmost left marginal plate.
14. Presence (1) or absence (0) of dorsal ornament.
15. Outline of the head asymmetrical (1) or symmetrical (0).
16. Mouth opening perpendicular to the longitudinal axis of the tail (1) or not (0).
17. Presence of two (2), three (0), four (1) or five (3) plates on the left side of the head.
18. Presence of three (0), four (1) or five (2) plates on the right side of the head.
19. Presence (1) or absence (0) of a fringe of striations along the external margins of the lateral marginal plates.
20. Presence (1) or absence (0) of D11.
21. D10 absent (0) or present and in contact with the most anterior four (1) or three (2) left marginal plates.
22. Presence (1) or absence (0) of an oblique ridge complex.
23. D12 in contact with the two most anterior right marginal plates and separated from remaining right marginal plates by an area of polyplated integument (1) or by a single row of plates (2) or in contact with the three most anterior marginal plates and separated from remaining right marginal plates by a single element (3) or none of these conditions (0).
24. Presence (1) or absence (0) of area of polyplated integument left of oblique ridge complex.
25. D12 contacts the two rearmost left marginal plates posterior to the transverse level of D10 (2) or not (1).
26. Rearmost right marginal plate inserted between the second most posterior right marginal plate and h (1) or not (0).
27. D12 in contact with h (2) or not (1).

28. n absent (0) or present and excluded from (1) or included (2) in the frame of head marginal plates.
29. Dorsal stereom texture of lateral marginal plates divided into a labyrinthic and a retiform region (0) or entirely labyrinthic (1) or compact (2).
30. Stereom texture of dorsal head skeleton retiform (0) or labyrinthic (1) or compact (2).
31. b and c delimit dorso-lateral parts of upper lip (1) or not (0).
32. Anterior margin of  $\varepsilon$  and  $\theta$  rounded (1) or polygonal (2).
33. Transverse axis of  $\varepsilon$  and  $\theta$  longer (1) or shorter (2) than longitudinal axis.
34. External stereom texture of  $\varepsilon$  and  $\theta$  divided into two transverse areas with different histology (1) or not (2).
35. Posterior margin of  $\varepsilon$  and  $\theta$  with median excavation (1) or not (2).
36. Anterior and antero-lateral margins of both  $\varepsilon$  and  $\theta$  without (1) or with (2) fringe of striations.
37.  $\varepsilon$  and  $\theta$  overlap rearmost lateral marginal plates (1) or scale-like elements comprised between them and the rearmost lateral marginals (2) or form sutures with both the scale-like elements and the rearmost lateral marginals (3) or are sutured with the lateral marginals only (4).
38. Lateral line opening absent (0) or present and sub-circular (1) or groove-like (2) or branched (3).
39. Presence (1) or absence (0) of plate p.
40. Presence (1) or absence (0) of placocystid plate.
41. Presence (0) or absence (1) of a strut bar.
42. Ventral ornament absent (0) or present and not extending (1) or extending (2) in front of  $\varepsilon$  and  $\theta$ .
43. Postero-ventral tessellate bar absent (0) or present and with admedian elements separated (1) or not (2) by p.
44. Oral platelets absent (0) or present and framed posteriorly by a semicircular band of small integument plates (1) or not (2).
45. Anterior margin of oral platelets tooth-like (1) or not (2).
46. Ventral head skeleton with a central region of larger plates with two lateral, narrow longitudinal strips of polyplated integument with numerous small (1) or few elements (2) or none of these conditions (0).
47. All ventral plates arranged in transverse rows (1) or not (0).
48. All ventral plates tessellate (1) or not (0).
49. Stereom texture of ventral head skeleton retiform (0), labyrinthic (1) or compact (2).
50. Presence (1) or absence (0) of ornament on the ventral projections of the lateral marginal plates.
51. Dorsal and ventral fore-tail plates meet along a flexible (1) or rigid (2) suture.
52. Presence (2) or absence (1) of thickening along posterior margin of dorsal fore-tail plates.
53. Presence (1) or absence (0) of spike-shaped plates on dorsal surface of fore tail.
54. Presence of multiple cusps (1) or two blades (2) on the styloid.
55. Anterior styloid blade with rounded profile (1) or not (2).
56. Anterior and posterior margins of posterior styloid blades cutting (1) or posterior surface of posterior blade flat (2).
57. Posterior styloid blade taller than anterior blade (2) or not (1).
58. First hind-tail ossicle with postero-dorsal bearing surface (2) or cutting (1) edges.
59. Ventral mid-tail plates absent (0) or present and separate from (1) or in contact with (2) the styloid.
60. Ventral margins of hind-tail plates meeting at an acute angle (1) or forming a continuous bearing surface (2).
61. Proximal hind-tail ossicles with bearing surfaces (2) or cutting edges (1).
62. Dorsal longitudinal canal of hind-tail absent (0) or present and partially (1) or completely (2) separated from hind-tail lumen.
63. Presence (1) or absence (0) of fibrillar stereom near dorsal margin of styloid blades and hind-tail ossicles.
64. Presence (1) or absence (0) of specialized olfactory areas.
65. Hypocerebral processes absent (0) or present and delimiting an optic foramen facing ventrally (1) or postero-ventrally (2).
66. Resorption areas of dorsal skeleton absent (0) or present and not forming (1) or forming (2) extensive fields over the two pharynges.
67. Anterior part of oblique ridge straight (1) or convex rightward (2).
68. Nerves n4 and n5 not differentiated (0) or differentiated and separated distally (2) or not (1).
69. Dorsal head skeleton completely flat (1) or not (0).
70. n subtrapezoidal and with posterior margin longer (1) or shorter (2) than anterior margin.
71. D12 contacts most of the posterior margin of n (2) or its right posterior angle (1) or none of these conditions (0).